

A REVISION OF THE HOUSTONIA PURPUREA GROUP
(RUBIACEAE)

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(Continued from page 180)

One of the more striking examples of differences between geographically distant colonies was observed in a few plants transplanted from Chautauqua County, New York, to southern Ohio. The plants were grown for several months and overwintered. In winter they produced a number of short, erect, basal offsets. In contrast, plants from southern locations have merely a basal rosette in winter. There are, also, a few other differences between northern and southern plants. Either the differences vary gradually and apparently clinally from north to south, or else they vary in an irregular manner; the natural existence of races and ecotypes is not apparent. For such reasons, it seems desirable to leave *H. canadensis* as a heterogeneous species without recognizing within it any infraspecific taxa.

This species intergrades with *H. purpurea* var. *calycosa* in southern Ohio, in Clark County, Indiana, and in central and western Kentucky. It is believed that these are actual hybrids. That the two species may occur together without producing intergrades was suggested by one observation made in Rowan County, Kentucky. Like other members of the *H. purpurea* group, the two taxa may sometimes cross, sometimes not. A lack of suitable intermediate habitats ("hybridization of the habitat" of Anderson) may not be the factor restricting survival of intermediates.

H. canadensis in its typical form is distinct from all other taxa and may usually be distinguished by the following combination of characters: stem with 3-6 internodes; lower and/or middle internodes conspicuously longer than upper ones; basal leaves conspicuous, pubescent above and ciliolate, persisting through the fruiting stage; cauline leaves oblanceolate, elliptic, or obovate, usually on one plant at least one pair of the middle and upper cauline leaves are widest near the apex, and often most

of the leaves are widest near the apex; calyx-lobes 1.6-3.5 mm. long.

General differences between this species and *H. longifolia* var. *longifolia* were illustrated rather well by John Torrey in his *Flora of the State of New York*, Vol. 1, Plate 44, 1843.

The following collections from northern Illinois are intermediate between *H. canadensis* and *H. longifolia* var. *longifolia*: KANE: Aurora, Boyce, June 1885 (GH). LASALLE: Starved Rock, Greenman et al, 1-7 June 1909 (F, GH, IA, NY); Starved Rock, Umbach, 29 May 1901 (F, WIS). WILL: Joliet Mound, Skeels 214 (F, GH, NY, US). In Ogle County one collection from Oregon, Gates 2723 (MICH), is closer to *H. canadensis*, but other collections from this county cited under var. *longifolia* are typical of that taxon. The writer collected (Terrell 2308) at Starved Rock State Park in LaSalle County in 1951, and confirmed to his own satisfaction that this population is intermediate. Two other collections from other states definitely suggest intermediacy between these same two taxa: **New York**. GENESEE: LeRoy, Hill, 7 July 1893 (F). **Michigan**. ST. JOSEPH: Three Rivers, Wheeler & Yoohida, 5 June 1890 (US).

One Wisconsin specimen of nearly typical *H. canadensis* is believed to be an error in location; in spite of intensive collecting in this state no later records exist: MONROE: Sparta, Hale, 1861 (F). Another sheet in herb. wis with an identical inscription is var. *longifolia*.

REPRESENTATIVE COLLECTIONS: — **Ontario**. BRUCE: damp sandy shores of Lake Huron, Red Bay, Stebbins et al 209 (CU, GH, WVA); Frog Island no. 16, Grassl 4954 (MICH); Stokes Bay, Krotkov 9416 (NY, US); Sauble Beach, Gleason, 20 June 1934 (DUKE). LINCOLN: Queenstown Hts., Wilkinson, 12 June 1886 (OC). NORTHUMBERLAND: Marie-Victorin et al 46014 (F, GH). **New York**. CHAUTAUQUA: Chautauqua Gorge, Muenschler & Brown 21709 (CU). MONROE: gorge of Genesee R. at Rochester, Matthews 2807 (NCU). NIAGARA: Niagara Falls, Lorenz, June 1916 (NCSC). **Pennsylvania**, WESTMORELAND: Big Pucketa Cr. near Parnassus, Patterson, 19 May 1915 (MO). **West Virginia**. TYLER: Middlebourne, Core 4126 (WVA). **Michigan**. ALPENA: stony flat, Thunder Bay Island, Ehlers 3172 (MICH, WIS). PRESQUE ISLE: Thompson's Harbor, Hinshaw, 14 June 1931 (MICH). WASHTENAW: Ypsilanti, Billington, 19 May 1919 (MICH). **Ohio**. ERIE: Castalia, Moseley, 28 May 1922 (GH, MICH, OS). FRANKLIN: Georgesville, Osburn, 4 May 1895 (OS). LAKE: Madison, Werner, 25 May 1885 (NY, OS). **Indiana**. CLARK: 3 mi. NW of Henryville, Deam 55770 (IND.) **Kentucky**. CARTER: Tygarts Creek, Braun 1707 (BRAUN); near Carter Caves, Gilbert, 20 May 1939 (GH). JESSAMINE: High Bridge, King 47 (F); Camp Nelson, McFarland 110 (MO, US). LINCOLN: 3 mi. SE of Crab Orchard, Wharton 2085 (NCSC); near Stan-

ford, *Biltm. Herb.* 7899b (US). PULASKI: just N of Burnside Bridge, *Terrell 1915* (CU). Tennessee. MARION: below Hales Bar Dam, *Fairchild et al 48-93* (TENN). WHITE: W of DeRossett, *Weatherby & Weatherby 6257* (GH, NY, TENN).

3. *Houstonia tenuifolia* Nutt., Gen. 1:95. 1818.

Hedyotis longifolia (Gaertn.) Hook. β *tenuifolia* (Nutt.) T. & G. Fl. N. Am. 2:40. 1841.

Oldenlandia purpurea (L.) Gray var. *tenuifolia* (Nutt.) Gray ex Chapman, Fl. S. U. S. 181. 1860.

Houstonia longifolia Gaertn. β *tenuifolia* (Nutt.) Wood, Class-Book, ed. 1861. 403. 1861.

Houstonia purpurea L. var. *tenuifolia* (Nutt.) Gray, Syn. Fl. N. Am. 1 (2):26. 1884.

Chamisme tenuifolia (Nutt.) Nieuwl. Am. Midl. Nat. 4:92. 1915.

Houstonia tenuifolia Nutt. f. *leucantha* Standley, Rhod. 34:177. 1932.

Hedyotis Nuttalliana Fosberg, Va. Jour. Sci. 2:111. 1941.

Hedyotis purpurea (L.) T. & G. var. *tenuifolia* (Nutt.) Fosberg, Castanea 19:35. 1954.

Hedyotis purpurea var. *tenuifolia* f. *leucantha* (Standl.) Fosberg, l. c. 36. 1954.

Perennial herbs. Rhizomes simple or branched, erect or horizontal, shortened or to 3.5 cm. long, bearing many small roots. Stems erect or ascending, one-several, round-tetragonal, (0.8-) 1-4 (-5.7) dm. high, densely cinereous-puberulent below, especially at nodes, with hairs on internodes usually less than 0.2 mm. long, or varying to glabrate. Internodes numbering (3-) 4-9 (-11); median internodes 3-6 (-8) cm. long. Nodes usually swollen. Stipules broad-ovate or broad-deltoid to ovate-lanceolate, entire, erose, or few-toothed at apex, often with dark glands at apices of teeth, obtuse, acute, or acuminate, to 4 mm. long, to 3 mm. wide; upper stipules often irregularly lobed. Basal leaves forming a rosette in winter, sometimes withered at time of flowering or sometimes persisting through flowering and fruiting (especially in plants of Missouri and Arkansas), varying from oval to spatulate, tapering into petioles shorter than to rarely longer than blades, to 3 cm. long, to 1 cm. wide, glabrous below, glabrous or sparsely pubescent above, sometimes sparsely ciliolate. Cauline leaves 1-nerved; lower leaves sessile or short-petiolate, oblanceolate to elliptic to linear; median leaves sessile, linear to narrowly elliptic or very narrowly oblanceolate, 1.3-4.7 cm. long, 0.5-4.0 (-5.0) mm. wide, usually at least 7 times longer than wide, glabrous below, glabrous or scabrous-pubescent above; upper leaves similar, smaller. Branches ascending, spreading, divaricate, or deflexed, slender and often ultimately filiform, usually with 1-4 remote nodes bearing reduced leaves, to 20 (-28) cm. long, usually arising from uppermost 3-6 nodes and forming a very diffusely open, few-very many

flowered inflorescence; often main stem equal in thickness to its branches, each node therefore appearing to give rise to 3 fertile branches. Pedicels filiform or slender, to 14 (-20) mm. long. Calyces glabrous; calyx-lobes erect, lanceolate, linear-lanceolate, or deltoid-lanceolate (0.5-) 0.8-2.4 (-3.0) mm. long, 0.2-0.9 mm. wide, less than one-half as long as corolla-tube, equalling or slightly exceeding mature capsules. Corollas purplish to white or variously purplish-tinged, (5-) 6-9 mm. long, granular to puberulent (rarely villous-pubescent) within; corolla-tubes 3-6 mm. long, 1.5-3.0 mm. wide distally; corolla-lobes 1.5-3.0 mm. long, 1.2-2.0 mm. wide. Mature capsules 1.5-2.5 (-3.0) mm. long, 1.5-2.5 (-3.0) mm. wide. Seeds 0.50-1.20 mm. long, 0.35-0.90 mm. wide.

Time of flowering: Late April or May through July. Earliest recorded flowering date is in late April; latest date is in late August. Fruits from the earliest flowers mature in July or August and continue to mature in order of development through summer and autumn.

Type locality: "Near the confluence of Pidgeon river, and the French Broad, Tennessee, on dry gravelly hills".

Type: Not seen.

Habitats and distribution: Dry or somewhat mesic woods of oak, oak-hickory, oak-pine; thin soil over various kinds of rocks; talus slopes; crevices in cliffs; openings and woodland borders. Commonly in open or lightly shaded places in well-drained, xeric-mesic habitats. Northwestern, southeastern, and southwestern Virginia; Fayette County, West Virginia; in North Carolina locally abundant in the Piedmont (where often around granite outcrops) and in French Broad drainage in Madison and Haywood Counties (Great Smokies); scattered and local in Piedmont of South Carolina; frequent in Cumberland Mountains of southeastern Kentucky and in Great Smokies of Tennessee; northwestern Georgia and adjacent Tennessee south to Heard County, Georgia; central Alabama; southern half of Missouri, northern half of Arkansas, and Leflore County, Oklahoma (mainly in Ozarks and Ouachitas); Ozark Hills of southern Illinois and adjacent westernmost Kentucky. (Map 2)

Nuttall's description is unequivocal for this species. His type has not been located, although specific attempts were made to

check the herbaria of the Philadelphia Academy of Natural Sciences, the New York Botanical Garden, and the British Museum.

This species has two main centers of distribution — the Appalachians and the Ozarks-Ouachitas. It appears to be absent from the territory between these centers. In the Appalachians it is locally disjunct and is absent in some areas which seem to have suitable habitats for it. It was reported from Texas and Mexico by Standley (1918), but no specimens have been seen from either. Shinnars (1949) stated that he had not seen any specimens from Texas.

Within this species typical Appalachian and typical Ozark-Ouachita plants differ as follows:

<i>Ozark-Ouachita</i>	<i>Appalachian</i>
Internodes 4-7	Internodes 4-9
Basal leaves often conspicuously large and sparsely ciliolate	Basal leaves usually smaller and glabrous
Middle cauline leaves averaging slightly wider-narrow-elliptic	Averaging slightly narrower-linear or very narrowly elliptic
Branches usually less than 10 cm. long, erect or ascending	Usually 9-20 cm. long, more often spreading to divaricate
Pedicels less than 8 mm. long	Less than 14 mm. long
Calyx-lobes longer, 1-2.4 (-3.0) mm. long	Shorter, 0.8-1.5 (-2.3) mm. long
Capsules larger, 1.5-3 mm. long	Smaller, 1.5-2.5 mm. long

This comparison is based on typical plants. Plants from Alabama and Georgia tend to be somewhat more like the Ozark plants. A number of collections from the two centers are very similar, e.g., collections from Rich Mountain, Arkansas, have filiform branches or pedicels like many Appalachian collections. Some piedmont, North Carolina, collections are very similar to Ozark collections. In general, the degree of overlap is so great that I have preferred not to distinguish plants of the two centers as separate subspecies, but consider them all part of one variable species. In addition, it is possible that some of the differences may be environmental. It appears that populations in these two centers have been isolated from each other for a rather long time, long enough for certain differences to have arisen.

In the past collectors have not always been sure whether Ozark-Ouachita plants should be identified as *H. tenuifolia* or as *H.*

longifolia. That the plants have been more often referred to the latter is due, apparently, to their wider leaves and shorter branches as compared with the narrower leaves and "setaceous pedunculate" flowers (as described by Nuttall) of the Appalachian group. Within each group populations vary considerably from locality to locality; some of this may be environmental, while chance isolation of certain biotypes in certain local areas may explain other variation.

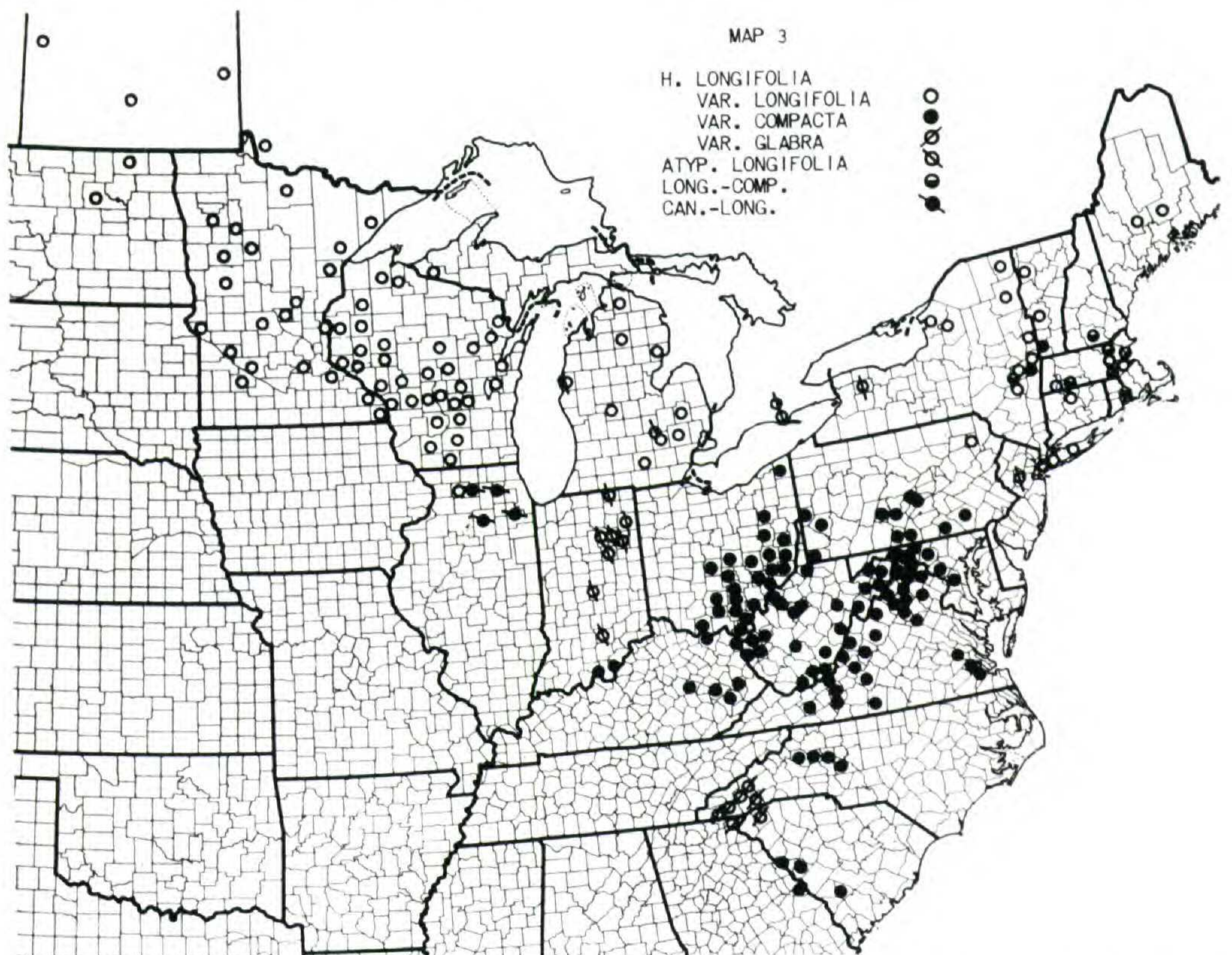
A collection from Walton Co., Florida, is quite atypical, being almost intermediate between this species and *H. longifolia* var. *compacta*. Since its characteristics are slightly more than those of *H. tenuifolia*, it has been placed in this species.

The relationship between this species and *H. longifolia* var. *compacta*, is another source of confusion in the *H. purpurea* group. It is sometimes very difficult to separate them, especially in herbarium collections which are not adequate samples of the population. At other times they appear quite distinct. It was formerly believed by the writer that they were two subspecies of the same species, *H. tenuifolia*, and on several occasions they were so annotated. Both taxa have densely cinereous-puberulent stems, and the cauline leaves seem basically similar although different in average length/width ratios. The writer was impressed, also, by the way they intergrade as one travels north from the Cumberland Mountains into the transitional counties of the Appalachian Plateau in eastern Kentucky. Two collections from Floyd and Morgan Counties seemed to indicate introgression into var *compacta*, while collections from Breathitt and Knott Counties indicate introgression into the other species. This is now interpreted as actual introgression, as originally supposed. Putative hybrids occur, also, in West Virginia and Virginia (cited below). However, introgression has not broken down the distinctness of these two taxa over large parts of their ranges. After observing how basically different they are in Alexander and Iredell Counties, western North Carolina, and in parts of southwestern Virginia, it was concluded that they should be placed in separate species. One of the more impressive differences is in time of initiation of flowering — this may differ by one to four weeks,

with two to three weeks being an average. In Alexander-Iredell counties they occur within 2½ miles of each other in rather similar habitats, but were not found growing together. In this area they appeared as different species, being different in as many as 6-10 characteristics.

Intergrades between *H. longifolia* var. *compacta* and *H. tenuifolia* include the following collections: **Virginia.** PAGE: roadside, Skyline Drive, 0.7 mi. s of Lewis Mt., *Walker 2923* (US). **ROCKINGHAM:** Swift Run, *Boettcher 501* (US). **West Virginia.** **FAYETTE:** Kimberly near mouth of Armstrong Cr., *Smithson*, 14 July 1936 (WVA). **GREENBRIER:** open upland woods, White Sulphur, *L. F. & F. R. Randolph 1291* (CU, GH). **MCDOWELL:** open woods between Barrenshe Cr. and Dry Fork, alt. 1350-1800 ft., *Morris 1162* (US).

REPRESENTATIVE SPECIMENS: **Virginia.** **CARROLL:** along New R. at mouth of Brush Creek, *Small*, 12 July 1892 (F, GH, MO, NY, PH, US). **MECKLENBURG:** 6 mi. N of Clarksville, *Fosberg 15441* (GH, TENN, WVA).



MAP 3. Distribution of the three varieties of *Houstonia longifolia*; atypical collections of var. *longifolia*; intergrades between var. *longifolia* and var. *compacta*; intermediates between var. *longifolia* and *H. canadensis*. Canadian collections of typical var. *longifolia* from vicinities of McKague, Saskatchewan, and Edmonton, Alberta, are not shown on map

SOUTHAMPTON: SW of Applewhite Church, *Fernald & Long 10431* (F, GH). **North Carolina.** ALEXANDER: 2½ mi. W of Vashti, *Radford 13868* (NCU). FRANKLIN: Cedar Rock, near Castalia, *Blomquist 13245* (DUKE). GRANVILLE: Oxford, *Godfrey 5473* (DUKE, NCU, US); 1 mi. S of Bullock, *Fox 4894* (NCSC). SURRY: Pilot Mt., *D. S. & H. B. Correll 14502* (DUKE). **South Carolina.** LANCASTER: Forty Acre Rock, *Ahles & Haesloop 27461* (NCU). **Georgia.** HEARD: 4 mi. SW of Franklin, *Pyron & McVaugh 1766* (GA). **Alabama.** CHAMBERS: *Earle*, 22 June 1897 (GH, NY). TUSCALOOSA: 15 mi. above Tuscaloosa, *Harper 3498* (GH, NY, US). **Kentucky.** HARLAN: near Harlan Court House, *Kearney*, Aug. 1893 (GH, MO, NY, US). HOPKINS: near Dawson Springs, *Palmer 17692* (MO, PALMER). **Tennessee.** BLOUNT: Cades Cove, *Anderson 1297* (GH, IA, MO). COCKE: Wolf Creek, *Kearney 736* (CU, MO, NY, US); vicinity Cosby, *Raper & Jennison 3296* (TENN). **Illinois.** JACKSON: 1½ mi. SE of Gorham, *Bauer 2698* (F). JOHNSON: 1.5 mi. S of Goreville, *Winterringer 984* (NCU). **Missouri.** BARRY: Eagle Rock, *Bush 100* (US, WVA); same loc., *Bush 15411* (WIS). HOWELL: Willow Springs, *Palmer 6228* (CU, F, MO). SCOTT: between Chaffee & Rockview, *Steyermark 5011* (F, MO). STODDARD: 2½ mi. W of Puxico, *Steyermark 66133* (F). **Arkansas.** CARROLL: Eureka Springs, *Palmer 5553* (CU, F, MO). LAWRENCE: Imboden, *Demaree 30444* (US). LOGAN: Magazine Mt., *Clausen 7661* (CU). **Oklahoma.** LEFLORE: Rich Mt., *Stevens 2667* (GH, MO, NY, US).

4. *Houstonia longifolia* Gaertner, Fruc. 1:226. 1788.

Houstonia longifolia Willd. Sp. Pl. 1 (2):583-584. 1798.

Houstonia longifolia Michx.; Torr. Fl. N. & M. U.S. 173. 1824.

Hedyotis longifolia (Gaertn.) Hook. Fl. Bor. Am. 1:286. 1834.

Anotis longifolia (Gaertn.) G. Don, Gen. Hist. 3:535. 1834. (in part)

Oldenlandia purpurea (L.) Gray var. *longifolia* (Willd.) Gray, Man. d. 2. 173. 1856. (in part)

Houstonia purpurea L. var. *longifolia* (Willd.) Gray, Man. ed. 5. 212. 1868. (in part)

Chamisme longifolia (Gaertn.) Nieuwl. Am. Midl. Nat. 4:92. 1915.

Hedyotis canadensis (Willd. ex R. & S.) Fosberg, Va. Jour. Sci. 2:110. 1941. (in part)

Hedyotis purpurea (L.) T. & G. var. *longifolia* (Gaertn.) Fosberg, Castanea 19:34. 1954. (in part)

Perennial herbs. Rhizomes branched or simple, horizontal or erect, sometimes subligneous, to 7 cm. long, bearing many small roots. Stems erect or ascending, one-many, tetragonal or roundish-tetragonal, sometimes slightly winged, 0.5–3.5 dm. high, densely cinereous-puberulent or pubescent or scabrous-pubescent below, especially at nodes, or glabrous. Internodes numbering (3–) 4–11 (–13); median internodes 1–5 (–6) cm. long. Nodes sometimes rather swollen. Stipules lanceolate to

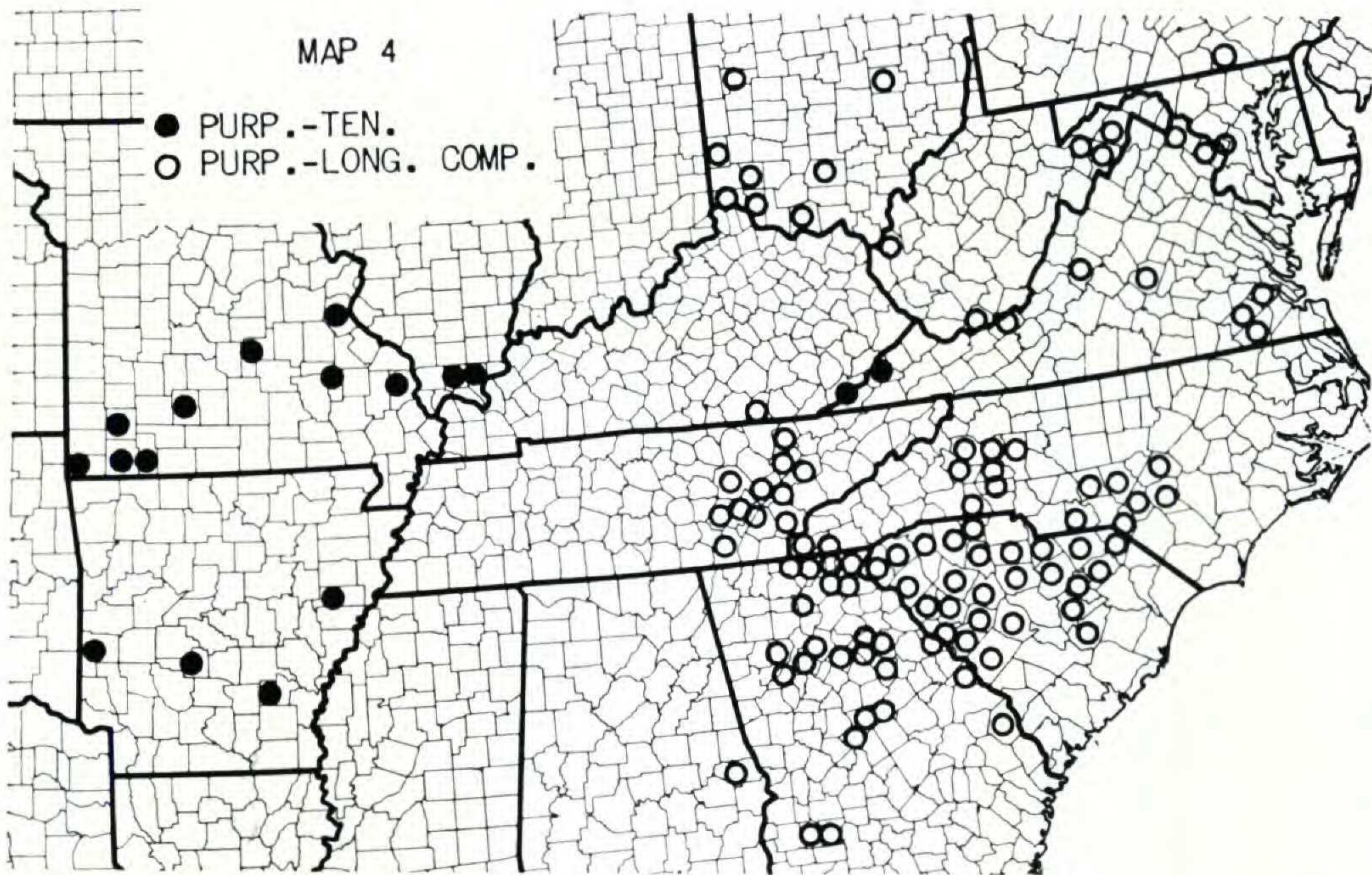
ovate, entire, erose, toothed (teeth often tipped with dark glands), or irregularly lobed, rounded above or varying from obtuse to acuminate, to 3.3 mm. long, to 3.5 mm. wide. Basal leaves forming a rosette in winter, sometimes persisting through flowering and fruiting or sometimes withered, oval, elliptic, or oblanceolate, tapering into petioles shorter or longer than blades, to 3.9 cm. long, 0.2–1.0 cm. wide, glabrous below, glabrous to sparsely pubescent above, sometimes sparsely ciliolate. Cauline leaves 1-nerved, lower ones sessile or short-petiolate; median leaves sessile, varying from narrowly elliptic to oblong to linear or very narrowly lanceolate or oblanceolate, 0.6–3.4 cm. long, 0.15–0.60 cm. wide, about 4–11 (–14) times longer than wide, glabrous below, glabrous to somewhat pubescent above, margins glabrous to sparsely ciliolate; upper leaves similar, smaller. Branches ascending or spreading, slender, less than 12 cm. long, forming a rather open to rather compact, few-many flowered inflorescence. Pedicels slender, less than 8 mm. long. Calyces glabrous; calyx-lobes erect or spreading, linear-lanceolate to ovate-lanceolate, (0.5–) 1.0–2.5 (–3.1) mm. long, 0.3–0.9 mm. wide, less than two-thirds as long as corolla-tube, equalling to somewhat exceeding mature capsules. Corollas white to purplish or variously purplish-tinged, (4–) 5–8 (–9) mm. long, granular to puberulent within; corolla-tubes 3–6 mm. long, 1.5–4.5 mm. wide distally; corolla-lobes 1.5–3.5 mm. long, 1.2–2.5 mm. wide. Mature capsules 1.7–3.8 mm. long, 1.7–3.3 mm. wide. Seeds 0.50–1.40 mm. long, 0.35–1.00 mm. wide.

Gaertner described only fruits and seeds of *H. longifolia*. None of the included drawings or descriptions can be applied with certainty to any particular member of the present group. One drawing was of calyces with rather short lobes and could not have depicted *H. purpurea* var. *calycosa*. The phrase, "Ex herbario Banksiano", was the only hint as to the source of Gaertner's plants. This suggested to the present writer that Joseph Banks was the collector, and that the type might be located either in the herbaria of Gaertner or Banks.

The location of Gaertner's herbarium apparently is unknown even to taxonomists in Europe. Correspondence with the British Museum, which has the herbarium of Banks, elicited the reply that no specimen resembling the type was to be found there. The remaining possibility is that the type may yet be found in other collections by Banks, which are known to exist in two other herbaria in Europe.

Although the original description is ambiguous and cannot

be applied with certainty, I prefer to retain Gaertner's name until all possibilities of finding the type material are exhausted. To replace this name with a new one would seem now slightly premature and would upset established nomenclature perhaps unnecessarily.



MAP 4. Distribution of intergrades between *Houstonia purpurea* and *H. tenuifolia* and between *H. purpurea* and *H. longifolia* var. *compacta*.

Willdenow's description in 1798 cited Gaertner's publication and followed the citation with a question mark, from which it appears that Willdenow was uncertain whether his plants were taxonomically equivalent to those of Gaertner. This implies, also, that Willdenow never saw the specimen described by Gaertner. Although included above as a synonym, Willdenow's description is hardly adequate. I consider it *probable* that he referred to the plants included by modern authors in *H. longifolia*.

The second synonym listed is believed to have resulted from Torrey's having erroneously ascribed the name to Michaux. Torrey cited Willdenow's publication first; perhaps he intended to put his name in place of "Mich." In his *Flora Boreali-Americana* Michaux did not mention *H. longifolia*, and no other mention of this name by him has been found. Torrey cited as another

synonym, *H. angustifolia* Michx., but we now know that this name is a synonym of *H. nigricans* (Lam.) Fern., a species outside the present complex.

In Hooker's description the mention of certain northern locations (Lake Huron, Lake Winnipeg, and Saskatchewan) leaves little doubt that he was describing *H. longifolia* in its strictest modern sense (group 1, as listed below).

The first part of Don's description was the same as Hooker's. An added series of phrases applied to *H. nigricans*, except that no member of the genus has "flowers scarlet."

In Gray's Manual, ed. 2, the concept is much like that of modern authors, except that Gray added, "A narrow-leaved slender form is *H. tenuifolia* Nutt." In edition 5 the same description was repeated under a new combination.

Fosberg (1941) used the name, *Hedyotis canadensis*, as including both that species and *H. longifolia*. Fosberg's (1954) combination was based on the judgment that the species of the *H. purpurea* complex were all varieties of one species.

H. longifolia Gaertner has in recent usage been so circumscribed as to include a variety of elements. These have seemed to intergrade in such a closely interwoven way that there is little wonder that they were never separated. This motley assortment has included what are believed to be hybrids and *H. longifolia* has served as a receptacle for many specimens that could not be referred to another species. After examination of herbarium specimens and after field observations and study of the populations region by region, it is possible to break down the conglomeration into the following morphological-geographical groups:

Group 1. A variable and heterogeneous series of populations ranging from New England across the Great Lakes states west to North Dakota and southern Canada to Alberta. These are restricted entirely to glaciated territory. Certain populations seem to intergrade with other taxa. This group along with groups 2 and 3 really constitute the main body of traditional *H. longifolia*.

Group 2. Alleghenian and central Appalachian populations

ranging south to South Carolina and Georgia. These are superficially somewhat like group 1 although less variable. Occasional specimens have been identified by collectors as *H. tenuifolia*, with which it intergrades. It intergrades also with group 5.

Group 3. Essentially very similar to group 2. Restricted to southern Blue Ridge.

Group 4. Ozark and Ouachita populations. Usually referred to *H. longifolia* but sometimes to *H. tenuifolia*.

Group 5. Variable populations in southeastern Virginia, North and South Carolina, Georgia, and Tennessee. Mainly in coastal plain and piedmont.

Group 6. Scattered miscellaneous populations elsewhere which resemble one of the other groups closely but have no definite continuous ranges.

TABLE 1 — Comparison of three varieties of *Houstonia longifolia*.

var. <i>glabra</i>	var. <i>compacta</i>	var. <i>longifolia</i>
Stems glabrous or glabrate	Densely puberulent	glabrous to pubescent
No. of internodes: 7-10	6-13	4-7
Stipules often lanceolate, acuminate, smaller	same as <i>glabra</i>	ovate, rounded or obtuse, larger
	These two differ by other "tendencies"	
In aspect, much like <i>compacta</i>		
These two allopatric, but only 50-75 miles apart; both southern and Appalachian; non-intergrading		
	These two with slightly overlapping ranges and a few intergrading populations; otherwise occupying large territories and well-separated geographically; one southern, one northern in glaciated territory	
Higher altitudes; mesic habitats in s. Blue Ridge	Lower altitudes; xeric-mesic; centered in Appal. Plateau and Ridge and Valley	Northern low alt.: xeric-mesic
Least variable	Rather variable; Intergrades with <i>H. purpurea</i> and locally with <i>H. tenuifolia</i>	Quite variable and heterogeneous, due to suspected former hybridization

In the present classification these groups are dealt with as follows: Group 1 — *H. longifolia* var. *longifolia*; Group 2 — *H.*

longifolia var. *compacta*; Group 3 — *H. longifolia* var. *glabra*; Group 4 — part of *H. tenuifolia*; Groups 5 and 6 designated as putative hybrids or hybrid races, in most of which the parental taxa are believed to be *H. purpurea* x *H. longifolia* var. *compacta* (these discussed in Introduction).

Table 1 points out the nature of the three varieties as well as the differences by which they can be distinguished. The status of var. *glabra* and its relation to var. *compacta* are further elucidated under the former variety. These two varieties are not as well differentiated from each other as are vars. *compacta* and *longifolia*. The latter two are almost subspecifically distinct.

4. *Houstonia longifolia* Gaertn. var. *longifolia*.

Stems 0.5–2.5 dm. high, glabrous to sparsely pubescent or sparsely scabrous-pubescent below, rarely somewhat puberulent. Internodes numbering (3–) 4–7; median ones 1–5 cm. long. Stipules of median nodes more or less ovate, rounded above, or varying from obtuse to acuminate, to 3.3 mm. long, to 3.5 mm. wide. Median cauline leaves narrowly elliptic, oblong, narrowly lanceolate, narrowly oblanceolate, or sublinear, (0.6–) 0.8–2.3 (–3.1) cm. long, 0.2–0.6 cm. wide, 4–10 times longer than wide. Mature capsules 1.7–3.8 mm. long, 1.7–3.3 mm. wide.

Time of flowering: late May or June through July or August.

Type locality: unknown.

Type: not seen.

Habitats and distribution: Secondary, xeric-mesic, well drained habitats in open or lightly shaded places, usually where relatively free of competition. Sandy soil or thin soil over various kinds of rock strata; openings or lightly shaded places in woods; rock ledges; fields and roadsides; dry prairies. Maine and other New England states, south to Long Island, northern New Jersey, and northeastern Pennsylvania, west across New York, southern Ontario, Michigan, Indiana (atypical), northern Illinois, Wisconsin, and Minnesota, west-northwestward to northern North Dakota, Manitoba, Saskatchewan, and Alberta. (Map 3)

Despite considerable variability and heterogeneity in var. *longifolia*, it seems impossible to break down this group any further. The variant populations seem to intergrade impercepti-

bly. This taxon does not have any "new" characteristics but its elements have in common a *combination* of characteristics which serve to unite them. Although each characteristic may be present in at least one other species or in intergradants between species, no other taxon has the same combination of characteristics so consistently expressed in many populations.

Plants of central and western Canada and the north shore of Lake Superior may resemble *H. canadensis* superficially, but may usually be clearly distinguished. Actual intergrades are cited under that species. In much of Minnesota, Wisconsin, Michigan, western New York, Vermont, and Maine, the more or less typical forms of the variety predominate. On Long Island a depauperate, possibly environmental, form occurs. Certain collections from southeastern and eastern New York, southern Vermont, New Hampshire, and parts of Massachusetts intergrade with var. *compacta*. A very few other New England collections grade toward the New England segment of *H. purpurea* var. *calycosa*. Atypical collections from Indiana, Ontario, and elsewhere are cited below.

Collections representing intergrades with var. *compacta* include the following: **New Hampshire.** HILLSBORO: Sharon, *Blake*, 24 July 1909 (US). **Massachusetts.** HAMPDEN: Westfield, *Seymour*, 16 June 1914 (DUKE, GH, MO). MIDDLESEX: Reading, *Pease 1243* (GH). **New York.** ALBANY: Glenmont, *House 6586* (GH, NY).

The following are rather atypical, and suggest introgression: **Ontario.** NORFOLK: Charlotteville Twp., *Soper 2618* (GH); Saint Williams, *Marie-Victorin et al 46424* (CU, F, GH); Normandale, *Marie-Victorin et al 46377* (GH). OXFORD: Tilsonburg, *Herriot 48* (GH); Tilsonburg, *Macoun*, 22 June 1901 (GH, NY). **New Jersey.** SOMERSET: Watchung, *Moldenke 2516* (NY). **Michigan.** LIVINGSTON: Portage Lake, *Ehlers 3851* (CU); Edwin S. George Reserve, *Evans*, 6 June 1951 (MICH). MASON: Hamlin Lake, Ludington, *Chaney 9* (F, NY, US).

A series of populations present in several counties of central and northern Indiana are atypical and are exemplified by the following (locality of coll. omitted): ALLEN, *Deam 1012* (NY); *Deam 1145* (F, IND). HUNTINGTON: *Deam 45845* (IND). LAGRANGE: *Deam 15904* (F, IND). WABASH: *Deam 49102* (CU). WELLS: *Deam & Gleason*, 1 Sept. 1904 (GH); *Deam*, 26 June 1904 (IND, MICH, US, WVA).

REPRESENTATIVE SPECIMENS: — **Alberta.** county unknown, near Edmonton, *Moss 2855* (GH). **Saskatchewan.** county unknown, 6 mi. sw of

McKague, *Breitung*, 2 Aug. 1936 (NY). **Manitoba.** MARQUETTE: Birtle, *Macoun & Herriot*, 26 June 1906 (CU, NY). PORTAGE LA PRAIRIE: Portage la Prairie, *Macoun & Herriot*, 5 June 1906 (F, NY). WINNIPEG: Pointe du Bois, *Love & Love 5546* (US). **Ontario.** SIMCOE: Wasaga Beach, *Marie Victorin et al 46216* (CU, GH, OC). **Maine.** PENOBSCOT: Veazie, *Knight*, 10 June 1905 (WVA); Veazie, Penobscot R. valley, *Fernald 14586* (F); Bangor, *Mackenzie 3216* (NY). SOMERSET: Fairfield, *Fernald & Long 14589* (PH, US); banks of Kennebec R., Carratunk, *Norton*, 10 July 1925 (WIS). **Vermont.** CHITTENDEN: Rock Point, Burlington, *Grout*, 9 June 1894 (F, US). **Massachusetts.** MIDDLESEX: Stoneham, *Bean*, 13 June 1904 (US); spur of Horn Pond Mt., Woburn, *Moore 2700* (GH). **New York.** CLINTON: Clintonville Sandplain, *Rudd 790* (US). ESSEX: Lower Jay, *House 10267* (US). JEFFERSON: Limerick, *Crockett 7560* (GA); Brownsville, *Redfield*, 19 July 1873 (MO, NY). LEWIS: Natural Bridge, *House 7141* (GH). **Pennsylvania.** LACKAWANNA: 2 mi. NE of Moosic, *Glowenke 349* (GH). **Michigan.** CHEBOYGAN: s of Burt Lake, *Gates 15520* (F, MO, TENN); *Ehlers 4636* (CU); Indian R., *Gleason*, 23 June 1935 (DUKE); 5 mi. s of Indian R., *Erlanson 443* (MICH). CRAWFORD: vic. of Grayling, *Piper*, July 1922 (US); 10 mi. E of Grayling, *Voss 2161* (MICH). **Illinois.** OGLE (all Oregon): *M. B. Waite*, 29 June 1885 (DUKE); *C. B. Waite*, 23 June 1885 (NY); *M. B. Waite*, 23 June 1885 (US). **Wisconsin.** ASHLAND: *Fasset & Wilson 10137* (WIS). POLK: St. Croix Falls, *Schuetz*, 11 July 1888 (F, GH); *Burglehaus*, 4 July 1892 (US). WAUSHARA: *Stearns 715* (WIS). **Minnesota.** CARLTON: Jay Cooke Park, *Wiegand & Wiegand 2234* (CU, GH). CLEARWATER: Desoto Lake, Itasca Park, *Buell*, 3 July 1938 (DUKE, NCSC). HOUSTON: 3 mi. W of Houston, *Moore 15991* (GH, IA). ST. LOUIS: about 6 mi. N of Palo, *Lakela 2604* (GH, NY); sandy shore of Esquagama Lake, *Lakela*, 4 Aug. 1944 (DUKE); *Lakela 14208* (WIS). **North Dakota.** BENSON: Butte, *Lunell*, 1 July 1914 (F); *Lunell*, 23 June 1907 (NY); Leeds, *Lunell*, 10 June 1911 (US). CAVALIER: Langdon, *Rider 200* (F).

4b. ***Houstonia longifolia*** Gaertn. var. ***compacta***, var. nov.

Caules dense cinereo-puberuli infra. Internodia (6-) 7-11 (-13); media internodia (1.0-) 1.5-3.5 (-4.4) cm. longa. Stipulae mediorum nodorum semper fere acuminatae vel acutae.

Stems 0.7-3.5 dm. high, densely cinereous-puberulent below (sometimes minutely so), with hairs on internodes rarely more than 0.4 mm. long, or rarely glabrate. Internodes numbering (6-) 7-11 (-13); median ones (1.0-) 1.5-3.5 (-4.4) cm. long. Stipules of median nodes usually more or less lanceolate or deltoid, sometimes ovate, usually acuminate or acute, sometimes obtuse or rounded, to 3 mm. long, to 2.5 mm. wide. Median cauline leaves narrowly elliptic, narrowly lanceolate, or sublinear, (0.8-) 1.6-3.0 (-3.4) cm. long, 0.15-0.5 (-0.6) cm.

wide, 4-11 (-14) times longer than wide. Mature capsules 1.8-3.0 mm. long, 1.8-3.0 mm. wide.

Time of flowering: early June through August or September. Earliest date is in late May, latest in Mid-October. Fruits usually mature from September through October.

Type: F. A. Gilbert July 9, 1937; June 1939; dry field, Roland Park, Cabell County, West Virginia (GH!). Duplicates of this collection (as *H. longifolia* Gaertn.) are widely distributed to a number of herbaria as *Plantae Exsiccatae Grayanae* #987, (CU, DUKE, F, GA, IA, MICH, MO, NCSC, NCU, NY, PH, TENN, US, WIS, WVA).

Habitats and distribution: In openings and lightly shaded places in dry woods (usually oak, oak-pine, oak-hickory, red cedar); thin soil over shale, sandstone, or igneous rocks, rock ledges, talus slopes, shale barrens; fields and roadsides. It ranges from central Pennsylvania (and disjunct to eastern New York and adjacent Vermont where very local) and eastern half of Ohio (disjunct to southernmost Indiana — an atypical form), southward through Maryland, West Virginia, eastern Kentucky (except Cumberland Mountains), Virginia, inner piedmont of western North Carolina, to, where very local, inner Coastal Plain in South Carolina and adjacent Georgia. (Map 3)

Except for a very few collections, this variety is confined to unglaciated territory. It is most frequent and abundant in the Appalachian Plateau and in the Ridge and Valley Province and more or less replaces *H. tenuifolia* in similar habitats northward in the central Appalachians.

The type collection was chosen because it is typical and is also widely distributed to a number of herbaria.

The relation of this taxon to *H. tenuifolia* is discussed under the latter species.

The first two collections, cited below, are of this variety but occur well within the range of var. *longifolia*. In the same area of southern New England intergrades of these two taxa are found (cf. Map 3 and citations under latter variety).

The epithet, *compacta*, refers to the compact appearance of the present variety as compared with var. *longifolia*. This compact-

ness results from shortened internodes. At the same time this variety has a greater number of internodes.

REPRESENTATIVE SPECIMENS: **Vermont.** BENNINGTON: slope of Red Mt., Arlington, *Blanchard 24* (GH). **New York.** RENNELLAER: Curtis Mt., n. of Brainerd, *House 21472* (GH). **Pennsylvania.** BEAVER: Brady's Run Valley, *Bright 6712* (WIS). FRANKLIN: dry woods, *Drushel 8626* (MO, US). FULTON: 1.5 mi. s of Needmore, *Wahl 2580* (GH). HUNTINGTON: Stone Valley, *Muenschel*, 12 June 1920 (CU, US). JUNIATA: near Cocolamus, *Jennings*, 18 July 1908 (CU). **Maryland.** MONTGOMERY: Little Falls Brook, *Pennell 2437* (GH). **Virginia.** AUGUSTA: vicinity, Elliott Knob, *Allard 3264* (US). BATH: Va. Hot Springs, *Hunnewell 4800* (GH). ORANGE: Orange, *Killip 13241* (US). SHENANDOAH: shale barrens, *Allard 11777* (US). **West Virginia:** CABELL: Roland Park, 15 July 1935, *Gilbert 376* (CINC, CU, GH, TENN, US, WIS). HARDY: open thicket, *Allard 9401* (US, WVA); near Wardensville, *Hunnewell 12438* (GH). **North Carolina.** ALEXANDER: 1 mi. s of base of Rocky Face Mt., *Terrell 3122* (NCU). ROWAN: 3 mi. NE of Spencer, *Radford 14302* (NCU). **South Carolina.** BAMBERG: w of Denmark, *Ahles & Haesloop 25985* (NCU). **Ohio.** HARRISON: *Kellerman*, 5 July 1902 (OS). MEIGS: Salem Twp., *Jones*, 29 June 1935 (NY, OS). **Kentucky.** ESTILL: Estill Springs, *Anderson 333* (GH, IA). LEWIS: Kinniconick, *Fulford*, 6 Aug. 1931 (CINC); Ohio-Kinniconick divide, *Braun 4395* (BRAUN, NY).

4c. *Houstonia longifolia* Gaertn. var. *glabra*, var. nov.

Caulis glabri vel pubescentes solum ad nodos inferiores. Internodia 7-10; media internodia (1.1-) 2.0-4.5 (-6.0) cm. longa. Alia sicut var. *compacta*.

Stems glabrous or short-pubescent at nodes only of lower parts of stems. Internodes numbering 7-10; median ones (1.1-) 2.0-4.5 (-6.0) cm. long. Otherwise as described for var. *compacta*.

Time of flowering: June through August.

Type: E. E. Terrell 3095, crevices of rocks in exposed places and in moist loam in woods, summit of Whitesides Mountain, alt. 4900 feet, about 5 mi. northeast of Highlands, Jackson Co., North Carolina, July 1, 15. (GH).

Habitats and distribution: On or around moist, wet, or dry rock outcrops, ledges, cliffs, usually over granite; sometimes in moist woods or openings but then usually not far from rock outcrops. Southern Blue Ridge in southwestern North Carolina, adjacent Georgia, and adjacent South Carolina. Known from Macon, Jackson, Transylvania, Haywood, Clay Counties, North

Carolina; Rabun County, Georgia; Pickens County, South Carolina. This variety is restricted entirely to the Blue Ridge at higher elevations. It has been collected at elevations ranging from 2800 feet (854 meters) to 5700 feet (1738 meters). (Map 3)

Var. *glabra* was collected extensively during the summer of 1957, and the limits of its presently known range were ascertained. The areas of its greatest abundance in North Carolina are eastern and central Macon County, parts of Jackson County, and the higher sections of the Balsam chain in Transylvania and Haywood Counties (where abundant along the Blue Ridge Parkway). The westernmost station is near the summit of Standing Indian Mountain along the border of Clay and Macon Counties. The southernmost stations appear to be the summits of Blackrock Mountain, Rabun County, Georgia, and Table Rock Mountain, Pickens County, South Carolina. The limiting factor in distribution may be the presence or absence of exposed rock (commonly granite) at higher altitudes. The Highlands area of Macon County and certain parts of neighboring counties have such habitats in abundance, but other sections of the southern Blue Ridge and Great Smokies either lack such habitats, or when such habitats are present var. *glabra* is absent.

Where the peaks of the southern Blue Ridge give way to the Piedmont Province in Rabun and Pickens Counties, plants judged to be hybrids of *H. purpurea* x *H. longifolia* var. *compacta* are present (see Map 4). These occur only at lower elevations and have not been seen growing with var. *glabra*; the two kinds of *Houstonias* seem to be isolated by altitudinal and habitat differences. At higher elevations in the Blue Ridge *H. purpurea* is widely distributed and often abundant. Although it and var. *glabra* were observed growing together at a number of places, no definite evidences of hybridization were seen. That one species may cross or has crossed with one variety of another species but not with the other variety of the second species is presumed to be explainable by the existence of much greater opportunity to cross with the first variety.

Various environmental modifications of var. *glabra* have been observed. In high altitude, exposed habitats it is more compact

and bushy. In shaded, sheltered places it is more elongate, with wider leaves, and whiter corollas. Differences in lengths of stems in two such contrasting habitats involve a change in lengths of internodes but no change in their total number.

As shown in Table 1, var. *glabra* differs from var. *compacta* by one morphological characteristic. The former variety is glabrous or nearly so — in plants growing on sunny, exposed rocks the lower internodes are so smooth they appear to have been polished. The latter variety has on the lowest internodes and nodes a dense covering of very short, grayish hairs which may be reduced to papillose protuberances visible at magnifications of 10-20 times. The single character difference is on the basis of nearly complete discontinuity: all plants within the geographic range of var. *glabra* are glabrous or short-pubescent only on the lower nodes; over 90% of plants within the range of var. *compacta* are densely puberulent or densely papillose. Those rare glabrate plants of the latter variety are sporadic and occur well to the north of var. *glabra*, there being no evidence at all of a lessening of the degree of puberulence southward.

Were the morphological difference the only difference in the two varieties, it would hardly be enough to set them apart as varietally distinct. They differ, also, in habitat: var. *glabra* grows generally in moist, humid places at higher altitudes, the other variety in dry places at lower altitudes. In addition, they are allopatric (cf. Map 3 and Table 1). The three kinds of differences setting var. *glabra* apart from var. *compacta* — morphological, ecological, geographic — are considered to indicate that it deserves status as a variety.

It may be questioned whether the morphological difference is an environmentally-induced one. Although this evidence is inconclusive, it may be noted that plants of var. *glabra* which were transplanted to about 1000 feet altitude in piedmont North Carolina in the fall of 1957 were glabrous in the summer of 1958.

REPRESENTATIVE SPECIMENS: **North Carolina.** HAYWOOD: top of Devils Courthouse, Beech Gap, *Corbin & Wyatt*, 14 Aug. 1954 (NCU). JACKSON: moist granite w of Cashiers, *Wherry & Pennell 14167* (DUKE); cliffs, Wild Cat Ridge, *Smith*, 21 August 1882 (GH). MACON: top of Fodder Stack, Highlands, *Sharp & Underwood 2877* (MO); Wild Cat Cliff

Highlands, *Oosting 1785* (DUKE, F. PH); Scaly Mt., *Godfrey 51413* (NCSC, US); Satulah Mt., *Biltm. Herb. 3974i* (NY, US); on Mt. Satula, Highlands, *Sharp 1369* (TENN); trail to Mt. Satulah, *McLean 110* (GA); trail and top of Mt. Satulah, *Oosting 34431* (OC); rock outcrop 5 mi. SE of Highlands, *Wilbur 1179* (DUKE). — Guilford College, North Carolina.

LITERATURE CITED

- CELARIER, R. P., AND K. L. MEHRA. 1958. Determination of polyploidy from herbarium specimens. *Rhod.* 60:89-97.
- FAGERLIND, F. 1937. Embryologische, zytologische und bestäubungs-experimentelle Studien in die Familie *Rubiaceae* . . . *Acti Horti Bergiani* 11:195-470.
- FERNALD, M. L. 1940. A century of additions to the flora of Virginia. *Rhod.* 42:355-416.
- . 1950. *Gray's Manual of Botany*. 8th ed., 1632 pp. New York: American Book Co.
- FOSBERG, F. R. 1937. Some *Rubiaceae* of southeastern Polynesia. *Bishop Mus. Occ. Pap.* 13:245-293.
- . 1941a. Observations on Virginia plants, part 1. *Va. Jour. Sci.* 2:106-111.
- . 1941b. Notes on Mexican plants. *Lloydia* 4:274-290.
- . 1943. The Polynesian species of *Hedyotis* (*Rubiaceae*). *Bishop Mus. Bull.* 174:1-102.
- . 1954. Notes on plants of the eastern United States. *Castanea* 19:25-37.
- GLEASON, H. A. 1952. *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada*. 3 vols. Lancaster, Pa.
- GRANT, V. 1957. The plant species in theory and practice, in *The Species Problem*. Symposium, ed. by E. Mayr. A. A. A. S. Pub. 50.
- LANJOUW, J., AND F. A. STAFLEU. 1956. *The Herbaria of the World*. 3rd ed. *Regnum Vegetabile* 6:1-224.
- ROBINSON, B. L., AND M. L. FERNALD. 1908. *Gray's New Manual of Botany*. 7th ed., 926 pp. New York: American Book Co.
- SHINNERS, L. A. 1949. Transfer of Texas species of *Houstonia* to *Hedyotis* (*Rubiaceae*). *Field and Laboratory* 17:166-169.
- STANDLEY, P. C. 1918. *Rubiales, Rubiaceae* (part) in *North American Flora* 32(1):24-38.
- . 1936. Studies of American plants — VI. *Field Mus. Pub. Bot.* 11:216.
- STEVENS, N. E. 1912. Observations on heterostylous plants. *Bot. Gaz.* 53:277-308.

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